Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*

Culum Brown and Victoria A. Braithwaite
Institute of Evolution, School of Biological Sciences, University of Edinburgh,
Edinburgh EH9 3JT, UK

Variable levels of predation pressure are known to have significant impacts on the evolutionary ecology of different populations and can affect life-history traits, behavior, and morphology. To date, no studies have directly investigated the impact of predation pressure on cognitive ability. Here we use a system of replicate rivers, each with sites of high- and low-predation pressure, to investigate how this ecological variable affects learning ability in a tropical poeciliid, *Brachyraphis episcopi*. We used a spatial task to assess the cognitive ability of eight populations from four independent streams (four high- and four low-predation populations). The fish were required to locate a foraging patch in one of four compartments by utilizing spatial cues. Fish from areas of low-predation pressure had shorter foraging latencies, entered fewer compartments before discovering the reward patch and navigated more actively within the maze, than fish from high-predation sites. The difference in performance is discussed with reference to forage patch predictability, inter- and intraspecific foraging competition, geographic variation in predation pressure, boldness–shyness traits, and brain lateralization. *Key words: Brachyraphis episcopi*, cognition, evolution, poeciliids, predators, prey. *[Behav Ecol 16:482–487 (2005)]*

I t is well known that the environment in which an animal lives has a compelling impact on the development and evolution of behavioral patterns, morphology, and life-history traits. Recently, researchers have become interested in the possibility that learning and memory are likewise adaptively specialized for the requirements of a species' way of life (Balda et al., 1998; Dukas, 1998). In general, animals that actively search for food, such as predators, tend to have larger brains than those animals that do not actively search for food (e.g., grazers), and this larger brain is related to the evolution of learning and memory capabilities. Food-storing birds, for example, have a greater capacity for spatial memory and possess a significantly larger hippocampus than closely related species that do not cache food items (Shettleworth, 2003). Similarly, animals that occupy spatially complex environments such as coral reefs also tend to have larger telencephalons (Kotrschal et al., 1988; Marchetti and Nevitt, 2003).

Through the use of the comparative approach it is possible to isolate particular aspects of the environment that are likely to contribute to differences in cognitive ability. Typically, closely related species that differ in various aspects of their lifestyle are chosen as experimental candidates in order to reduce the confounding effect of phylogenetic history (e.g., among the corvids; Kamil and Balda, 1990). An even better approach is to investigate populations of the same species sampled from contrasting habitats.

One well-documented environmental variable that is commonly compared among populations in different geographic locations is varying levels of predation pressure (Endler, 1995). Prey species living in the presence and absence of predators experience very different selective pressures, and these result in a suite of traits that clearly differentiate between themselves (e.g., life-history traits, Jennions and Telford, 2002; boldness–shyness scores, Brown and Braithwaite, 2004; predator avoidance responses, Magurran and Seghers, 1990). Could differences

in predation pressure drive divergence in the cognitive ability of individuals as well?

Our approach takes advantage of a natural field situation in which different populations of the same species of fish, *Brachyraphis episcopi*, are found in replicate streams, each containing regions of high- and low-predation pressure. These streams are all independent watersheds that flow directly into the Panama Canal, and given that our study species is confined to the headwaters of these streams, each represents an independent replicate system with which to investigate the effects of predation pressure on the cognitive ability of the fish. Each river flows over an escarpment and has one or more waterfalls that prevent upstream colonization of most fish species. Above the falls, the fauna almost entirely comprises *B. episcopi* and the killifish *Rivulus brunneus*. *B. episcopi* is also found below the falls but is accompanied by a suite of predatory species, including cichlids and tigerfish (*Hoplias panamensis*) (see Brown and Braithwaite, 2004, for further details). To take advantage of this abrupt change in the fauna while minimizing physical differences in other stream and site characteristics (physical parameters available for each site on request), we selected high- and low-predation sites that were around 100 m apart.

An ability to move around an environment in a directed fashion, either in search of food and mates or to avoid hazards such as predators, is a fundamental requirement of virtually all animals (Brown, 2003). A general capacity for spatial learning and memory can, therefore, be regarded as an advantageous skill, enabling animals to move efficiently within their environment and in some instances to plan their routes (Giraldeau, 1997; Healy, 1998). Furthermore, there is no evidence to suggest that specific spatial skills are required to track different objects in space (e.g., predators or prey); therefore, a generalized aptitude for spatial learning is likely to be applicable in all contexts.

Assays of cognitive ability frequently involve tests that quantify spatial learning and memory owing to its widespread applicability (Healy, 1998; Shettleworth, 1998). Analysis of spatial ability can provide at least two types of measures: first, the length of time taken to learn a particular spatial task, and
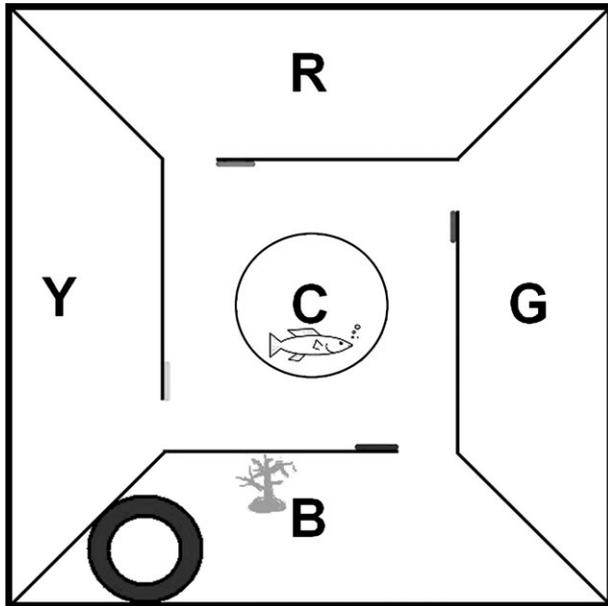
Figure 1
Diagram of the maze apparatus picturing the central compartment (C) with the clear cylinder housing the test fish. The feeding ring and the location of the plastic plant are shown in the blue compartment (B). The colored markers are shown in place adjacent to each of the four doors. The length and width of the aquarium was 46 cm, and the door opening was 5 cm wide.

second, the type of spatial information the animal uses to solve the spatial problem (Odling-Smee and Braithwaite, 2003a). Animals often differ in the cues they rely on to navigate within their environment, and these differences can often be traced back to cue availability and reliability within their local habitat (see Odling-Smee and Braithwaite, 2003b, for a review). For example, some individuals rely on beacons or local landmarks that directly indicate specific locations, while others rely on global cues where a location is calculated by the integration of the relative position of many cues (Warburton, 1990).

Many of the fish species within the streams we used, including *B. episcopi*, are opportunistic omnivores relying on a supply of fruit and insects falling from the canopy to provide a significant proportion of their diet (Angermeier and Karr, 1983). This contrasts with guppies, swordtails, and other poeciliids where algae are an important source of nutrition. Regions of relatively high flow deliver the greatest number of food items, and these locations are highly sought after. *B. episcopi* is an unusually aggressive and highly territorial poeciliid, but this behavior makes sense within the context of their diet and the environment that they occupy. Hierarchies form quickly in the laboratory with dominant females taking up position in the preferred feeding locations, and this also appears to be the case in the wild (Brown C, personal observation).

Keeping track of the location of feeding patches and territories is likely to play an important role in determining the location of and interactions between fish in a given pool regardless of whether these fish are from high- or low-predation locations. In either location, being able to learn about the distribution of resources in the environment will have considerable fitness benefits. In high predation, downstream areas, however, it is likely that fish will also use spatial information to enable them to avoid predators. Cognition has a neural basis, and brain tissue is the most expensive tissue for the body to maintain; therefore, it is likely that rigorous

Table 1
The GPS location of each of the sample sites[a]

Population	Location	GPS co-ordinates (N and E)
AS	Low predation	9° 12′ 52″, 79° 46′ 48″
AS	High predation	9° 12′ 49″, 79° 46′ 49″
QJG	Low predation	9° 08′ 37″, 79° 42′ 57″
QJG	High predation	9° 08′ 37″, 79° 43′ 00″
RL	Low predation	9° 09′ 54″, 79° 44′ 28″
RL	High predation	9° 09′ 38″, 79° 44′ 25″
RM	Low predation	9° 11′ 02″, 79° 45′ 36″
RM	High predation	9° 11′ 03″, 79° 45′ 42″

[a] GPS, Global Positioning System.

trade-offs between the relative costs and benefits associated with improved learning abilities exist (Mery and Kawecki, 2003). We might expect therefore that variation in predation pressure will drive divergence in cognitive ability, but predicting the exact nature of the effect is difficult. To determine if this was the case, we tested the spatial ability of fish from high- and low-predation sites using a five-chambered maze (see Figure 1) in which the fish were required to learn the location of a foraging patch.

METHODS

Subjects

B. episcopi were captured using dip nets in four streams (Rio Limbo [RL], Rio Macho [RM], Quebrada Juan Grande [Q JG], Rio Agua Salud [AS]), each containing an upstream low-predation and a downstream high-predation site (see Table 1 for Global Positioning System coordinates of each location). The fish were airfreighted to the University of Edinburgh and housed in 90-cm-long aquaria. Each aquarium was equipped with a power filter, plastic plants, gravel, and rocks. Water was maintained at approximately 26°C, pH 7, and overhead fluorescent lights provided 12:12 h light:dark. Fish were fed on a mixture of commercial flake and live food once per day. Although there are differences in the average standard length between fish from high- and low-predation sites (Brown and Braithwaite, 2004; Jennions and Telford, 2002), we minimized this by deliberately testing fish of approximately the same size from each population (mean standard length 40.7 mm).

Apparatus

The maze apparatus was inspired by Burt de Perera and Garcia (2003) and comprised a central compartment (33 by 33 cm) with four doors (5 cm wide) leading to four fringing compartments (see Figure 1). The dimensions of the maze tank were 46 by 46 cm, and water depth was maintained at 18 cm. Water temperature was similar to the stock tanks. Adjacent to each door, a colored marker (blue, red, green, and yellow) was placed to provide a discrete landmark to label each door. Initial preference tests utilizing the same fish tested herein suggested that the fish showed a strong preference for red, no preference for green or yellow, and avoided the compartment indicated by the blue marker (possibly because it was opposite the red compartment). There was little difference in color preference for upstream and downstream fish (chi square on first choice for all fish; $\chi^2 = 3.419$, df $= 3$, $p = .331$). Most importantly, three upstream fish and two downstream fish showed a first-choice preference for the compartment indicated by the blue tile. We
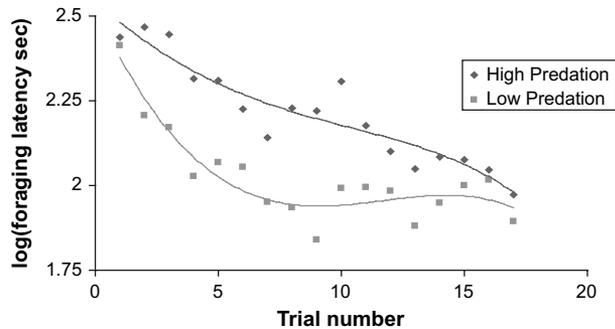
Figure 2
The forage latency of low- and high-predation fish over the length of the experiment.

have no reason to suspect that the fish could not perceive the colors on any of the tiles because fish inhabiting clear shallow waters typically have a broad visual capacity, seeing all the colors in the human visible spectrum as well as shorter wavelengths into UV (Endler et al., 2001; Smith et al., 2002).

In order to maximize the learned component of the task, the rewarded food patch and a plastic plant were placed in the least preferred compartment indicated by the blue marker. The feeding patch consisted of flake food and was contained within a floating feeding ring attached to the back wall of the compartment. The fish had no prior experience of feeding within the ring; however, its sole purpose was to prevent the flake food spreading out across the surface of the water. A plastic plant, similar to those in their housing tanks, provided shelter. The fish could not see the feeding ring or the plastic plant until they had entered the door, which measured 5 cm across. The maze was not covered, therefore, the fish could also rely on extra-maze cues outside the tank to aid their orientation; however, a white curtain placed on one side prevented the fish from being disturbed by other movements in the room. The maze was designed such that passive movement around the maze in an anticlockwise direction was encouraged, owing to the orientation of the internal walls. This increases the likelihood that the fish become familiar with all compartments in the maze relatively quickly. We used low lighting, with no lights directly shining into the maze, to enable the fish to settle quickly after being transferred into the maze.

Procedure

A random sample of six female fish from each population was chosen. The fish were housed individually in a numbered, clear plastic floating container. Each fish was gently transferred from its own container and placed into a clear start cylinder in the central compartment of the maze (Figure 1). The fish remained in the cylinder for 2 min before the cylinder was lifted clear of the maze, and the fish was free to move around at will. The fish's task was to locate the compartment containing the foraging patch. Fish were not offered food at any time other than when in the maze and were therefore motivated to discover the patch. The behavior of the fish was recorded by an overhead digital video camera linked to a laptop computer. A remote observer noted the location of the fish in real time using the Etholog 2.2 software. The number of doors entered before discovering the rewarded compartment was recorded, as was the time taken to begin feeding on the reward patch. The pattern of turn direction (left, right, return, or across) when emerging from each compartment was also noted and the proportion of right-hand turns made by the fish calculated. Fish were

deemed to have failed the test if they did not discover the food reward within 10 min and were allocated a ceiling foraging latency of 600 s and a door entry value of 15. The door entry ceiling value was set just above the highest number of door entries observed during the experiment. The fish were tested once per day for 18 days.

After the first day of observations, it became clear that not all fish entering into the correct arm visited the feeding patch; subsequently, we began to record the time to forage. We present data from days 2 to 18 for the time to forage and days 1 to 18 for all other variables.

Analysis

The data were log transformed where necessary before being subjected to repeated-measures ANOVA with stream and predator regime as fixed factors.

RESULTS

The mean time taken to locate the patch and begin feeding shows a marginal effect of predator regime ($F_{1,40} = 3.70$, $p = .061$), suggesting that over the period of the experiment low-predation fish were faster to locate the rewarded patch and begin eating than high-predation fish. Examination of Figure 2 shows that by day 10 low-predation fish had reached their minimum foraging latency, whereas high-predation fish only reach a similar level by day 18. When the data from days 2 to 14 only were analyzed, there was a significant difference between high- and low-predation fish ($F_{1,40} = 5.819$, $p = .021$). A marginal but nonsignificant interaction between stream and predator regime was observed ($F_{3,40} = 2.51$, $p = .07$), and post hoc analysis (Fisher's protected least significant difference) revealed that the differences between high- and low-predation fish were greatest in the AS and RM fish. There was also a significant difference in the latency to forage between the streams ($F_{3,40} = 3.445$, $p = .026$). RL fish were the slowest to discover the patch preceded by Q JG and RM, with fish from AS being the fastest. Fish from all streams showed improvements in foraging latency over the 18 days (repeated-measures ANOVA split by stream; $F_{16,160} = 3.398$, 1.703, 1.597, and 3.426; p, <.001, .051, .75, and <.001 for AS, Q JG, RL, and RM, respectively).

The results for the latency to forage data were further supported by the number of doors the fish passed through before entering the door containing the food patch. High-predation fish tended to enter more doors than low-predation fish ($F_{1,40} = 3.12$, $p = .08$) (Figure 3). Both low- and high-predation fish reduced the number of doors they traveled through to discover the patch over the length of the experiment ($F_{17,680} = 5.94$, $p < .001$). There were no differences between the streams in this measure.

The maze was assembled in such a way so as to encourage fish to move in an anticlockwise direction, particularly if the fish stay close to the walls. Therefore, a fish moving around the maze in an undirected manner should make many more right-hand turns when emerging from any given door than a fish moving about the maze in a directed fashion. Analysis of the proportion of right-hand turns made by the fish reveals that high-predation fish turned right more often than low-predation fish ($F_{1,38} = 5.44$, $p = .02$; Figure 4). Furthermore, there was a significant difference between rivers ($F_{3,38} = 4.16$, $p = .012$); RL fish turned right more frequently than RM and AS fish, with Q JG fish turning right least often.

The proportion of fish choosing red, yellow, or green colored doors as their first choice declined over the period of the experiment. Regression analysis revealed that the decline was only significant for the green and yellow doors ($p = .037$,
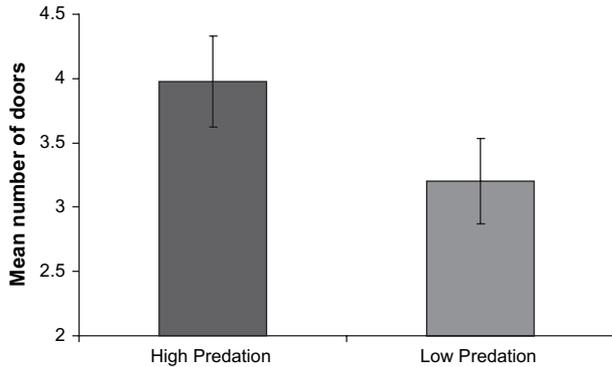
Figure 3
The average (±SE) number of doors fish from low- and high-predation locations passed through before discovering the foraging patch.
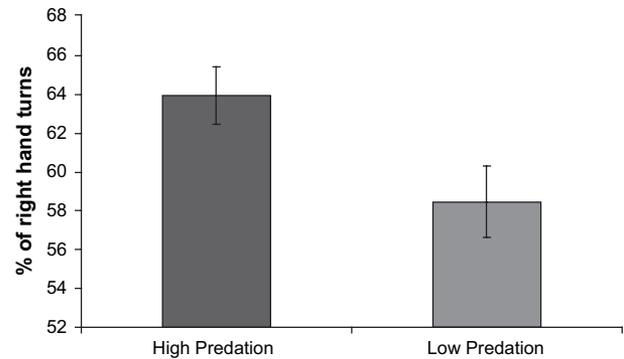
Figure 4
The percentage (±SE) of right-hand turn direction choices made by fish from low- and high-predation locations for the duration of the experiment.

.038, and .125 for green, yellow, and red, respectively). In contrast, the use of the blue door as a first choice rose steadily as the fish learned the location of the foraging patch (regression: $F_{1,16} = 53.53$, $p < .0001$). The pattern is similar for both low- and high-predation fish.

The number of fish failing to discover the foraging patch was low and had little bearing on the results. There were 25 incidences of failure in the high-predation fish and 15 in the low-predation fish (>5% of trials) over the entire experiment. Most of the failures occurred during the early trials. Two fish (one from each predation regime) failed eight times each.

DISCUSSION

Fish from low-predation sites solved the spatial task almost twice as quickly as fish from high-predation areas. Indeed, the analysis of the time to forage up to day 14 showed a significant difference between low- and high-predation fish. However, by the end of the 18 days, the performance of high-predation fish had reached a level similar to that of their low-predation counterparts. In general, low-predation fish traveled through fewer doors to discover the foraging patch and were faster to feed. The difference in their behavior within the maze is highlighted by the fact that the high-predation fish moved around the maze in a less directed fashion than the low-predation fish, as indicated by the higher proportion of right turns made by high-predation fish. Nonetheless, all fish showed a strong tendency to turn right as expected by the maze design.

There are several possible explanations for the differences in the performance of the fish in this task, and these are summarized below.

Population differences in cue use

Although this task may appear fairly simple, it should be noted that the location of the blue door and the food reward are spatially separated. In fact, the position of the food reward is closer to the yellow door than to the blue door (Figure 1). The global cues the fish perceive at the blue door and the foraging patch are therefore quite different, so it would be difficult to use the global cues at the door location for finding the location of the food unless they utilize the information as a way marker. In order to navigate around the maze efficiently, therefore, the fish should rely on the symbols next to the doors and try to ignore global information associated directly with the patch location. It was observed throughout the experiment that many

of the fish found it difficult to comply, spending much of their time swimming back and forth along the wall separating the blue and yellow compartments. On occasion, fish jumped the wall to gain access to the foraging patch.

It seems likely that fish from streams generally have a preference for using global cues because using a single local cue is less reliable due to an increased probability that the cue might move during periods of high flow (Brown, 2003; Girvan and Braithwaite, 1998). The evidence to suggest that fish from high- and low-predation areas rely on different types of cues to navigate within their environment is equivocal, largely because these differences are often confounded by other ecological variables (e.g., Huntingford and Wright, 1989). Water flow variability and clarity, for example, are two prime environmental components that may cause divergence in cue use in fish (Odling-Smee and Braithwaite, 2003b). In the present study, the sites within each stream were very close together and probably preclude the possibility of variation in the reliance of local versus global cues to solve the maze, owing to the similarities in the physical aspects of the two habitats. The main difference between sites within each stream was the composition of the in-stream fauna.

Predation and interspecific competition

Despite the fact that we have tended to concentrate on the presence or absence of predators, the majority of interactions between *B. episcopi* and the rest of the fauna in the high-predation sites are probably competitive rather than predatory in nature. Above the falls, only two species of fish exist, *B. episcopi* and the killifish *Rivulus brunneus*. In these regions *B. episcopi* dominates the fauna often comprising more than 90% of the fish captured (Brown and Braithwaite, 2004); therefore, intraspecific competition for access to food is very high. In the regions bellow the falls there are a myriad of competitors and predators alike, including three species of cichlids, tigerfish (*Hoplias microlepis*), 20 odd species of tetras (Characidae), and many others. In these streams, food items tend to fall randomly from the canopy onto the water surface, but locations with high water velocity deliver more prey items into a given area than low-velocity waters (Keeley and Grant, 1995; Nislow et al., 1998). In order to flourish, fish would benefit by being able to track the location of preferred foraging patches in both low- and high-predation locations. In the absence of other species, rigid dominance hierarchies form in *B. episcopi* populations and dominant fish occupy the preferred foraging locations. In the presence of both predators and interspecific competitors in high-predation

areas, *B. episcopi* are unlikely to occupy preferred foraging niches. One would expect the best foraging locations to be dominated by larger species including tetras and candlefish (*Piabucina panamensis*). It may well be that low-predation fish place a high priority on locating and dominating preferred foraging patches and hence solve the maze more quickly, whereas high-predation fish prioritize predator avoidance, are displaced from preferred foraging locations, and are restricted to relatively safe microhabitats. The apparent slower learning of the high-predation fish might reflect the different priorities of fish from high-predation regions. It might be advantageous for high-predation fish to thoroughly explore a new environment to locate potential refugia or escape routes or to ensure no predators are present. Thus, the longer latency to forage and the greater number of doors entered might suggest that the high-predation fish are trading off more efficient foraging for gathering more detailed information about the spatial layout of the environment than fish from low-predation areas. A task involving finding the location of a refuge when threatened rather than a foraging patch may reveal such differences in priorities. Further field experiments are also required to determine the microhabitat preferences of fish from both high- and low-predation areas as well as to compare the levels of aggression and territoriality.

Boldness and shyness

Population differences in temperament might be another possible explanation for our maze results. One of the major axes of behavioral variation in all animals, including humans, is the shyness–boldness axis (Wilson et al., 1994). In fishes, shyness can be scored in a number of ways, but it is generally described as the propensity to take risks, which may include behavioral traits such as neophobia. Theoretically, bold fish would begin exploring the maze sooner than shy fish and hence discover the location of the foraging patch more quickly. If upstream fish were bolder than downstream fish, then this could potentially explain why they perform so much better in the maze. Our measures of boldness of these fish in the laboratory, utilizing an open field paradigm, showed inconsistent differences between low- and high-predation sites (Brown and Braithwaite, 2004). However, examination of boldness traits in the field revealed that high-predation fish are bolder than low-predation fish in all rivers (Brown et al., unpublished data). If this is the case, then the estimates of the difference in spatial ability between fish from high- and low-predation sites outlined herein may be conservative because shy (low predation) fish should take longer to explore novel environments than bold fish.

Lateralization and turn preference

The propensity to turn right in this experiment provides one way of measuring fish performance within the maze; however, there are a number of things that may affect this behavior. It is well known that many fish species show biases in their turn preference due to variation in the extent of lateralization of the brain (Miklosi et al., 1997). Even within the Poeciliidae, intriguing variation between species exists in the propensity to turn right or left (Bisazza et al., 1997). Experiments using the same populations tested herein indicate that fish from low- and high-predation sites differ in their pattern of cerebral lateralization. High-predation fish viewed predators with the right eye and novel objects with their left eye, whereas no preference for eye use in low-predation fish was evident (Brown et al., 2004). Cerebral lateralization is manifested in turn biases in virtually all animals tested to date including fish (Vallortigara and Rogers, 2004). Whether this pattern of eye preference to view predators in our species translates into turn preference within the maze remains to be tested but seems highly likely.

Interstream differences

While there is an overall effect of predation pressure across all the streams, we did observe differences between the streams. There are a number of possible explanations for the observed differences in the behavior of the fish between rivers primarily pertaining to the larger ecological differences that occur at this scale. We deliberately chose streams and sites within streams to minimize the differences in geomorphological structure and in-stream fauna, but clearly the rivers were not identical. It is apparent that fish from Q JG, RM, and AS performed equally well in the maze task, whereas RL fish performed comparatively poorly. There is nothing particularly different about the RL, although it is more prone to drying out during the dry season due to its smaller catchment area. It is possible that during these dry periods, when there is little or no flow, the importance of maintaining a territory is reduced as the location of prey becomes less predictable and hence learning the location of the defendable resource becomes irrelevant. Furthermore, because catchment size is inversely related to habitat stability (Brown, 2003), it may be that flow is more variable in the RL. We have data loggers in place to examine this possibility. It is known that fish from different populations rely on different cues based on their relative stability (Girvan and Braithwaite, 1998). If so, fish from the RL should rely on global cues to navigate, and this also may explain their poor performance in the maze.

Despite the fact that there are differences in cognitive abilities of fish from each of the four streams examined, our results indicate significant differences between fish from high- and low-predation locations. Consistent differences in the amount of predation pressure and interspecific competition between upstream and downstream sites in each stream are the most likely explanations for the observed differences in cognitive ability. Other behavioral variables such as differences in temperament and brain lateralization probably influence motivation and turn bias within the maze, respectively. Owing to the close proximity of the high- and low-predation sites, cue use is unlikely to differ and therefore has little bearing on our results but may explain differences between rivers where larger ecological differences exist. Determining the relative role of predation pressure and interspecific competition in shaping the differences within each drainage system remains a primary topic for future investigation.

REFERENCES

Angermeier PL, Karr JR, 1983. Fish communities along environmental gradients in a system of tropical streams. Environ Biol Fish 9:117–135.

Balda BP, Pepperberg IM, Kamil AC, 1998. Animal cognition in nature. San Diego: Academic Press.

Bisazza A, Pignatti R, Vallortigara G, 1997. Laterality in detour behaviour: interspecific variation in poeciliid fish. Anim Behav 54:1273–1281.

Brown C, 2003. Habitat-predator association and avoidance in rainbowfish (*Melanotaenia spp.*). Ecol Freshw Fish 12:118–126.

Brown C, Braithwaite VA, 2005. Size matters: a test of boldness in eight populations of bishop, *Brachyraphis episcopi*. Anim Behav (in press).

Brown C, Gardner C, Braithwaite VA, 2004. Population variation in lateralised eye use in the poeciliid *Brachyraphis episcopi*. ProcR Soc Lond B 271 (Suppl.):S455–457.

Burt de Perera T, Garcia CM, 2003. Amarillo Fish (*Girardinichthys multiradiatus*) use visual landmarks to orient in space. Ethology 109:341–350.

Dukas R, 1998. Cognitive ecology. Chicago: Chicago University Press.

Endler JA, 1995. Multiple trait coevolution and environmental gradients in guppies. Trends Ecol Evol 10:22–29.

Endler JA, Basolo A, Glowacki S, Zerr J, 2001. Variation in response to artificial selection for light sensitivity in guppies (*Poecilia reticulata*). Am Nat 158:36–48.

Giraldeau LA, 1997. Ecology of information use. In: Behavioural ecology, 4th ed (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific.

Girvan JR, Braithwaite VA, 1998. Population differences in spatial learning in three-spined sticklebacks. Proc R Soc Lond B 265:913–918.

Healy S, 1998. Spatial representation in animals. Oxford: Oxford University Press.

Huntingford FA, Wright PJ, 1989. How sticklebacks learn to avoid dangerous feeding patches. Behav Process 19:181–189.

Jennions MD, Telford SR, 2002. Life-history phenotypes in populations of *Brachyrhaphis episcopi* (Poeciliidae) with different predator communities. Oecologia 132:44–50.

Kamil AC, Balda RP, 1990. Spatial memory in seed-caching corvids. Psychol Learn Motiv 26:1–25.

Keeley ER, Grant JWA, 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 52:186–196.

Kotrschal K, Van Staaden M, Huber R, 1998. Fish brains: evolution and environmental relationships. Rev Fish Biol Fish 8:373–408.

Magurran AE, Seghers BH, 1990. Population differences in predator recognition and attack cone avoidance in the guppy *Poecilia reticulata*. Anim Behav 40:443–452.

Marchetti PM, Nevitt GA, 2003. Effects of hatchery rearing in brain structures of rainbow trout, *Oncorhyncus mykiss*. Environ Biol Fish 66:9–14.

Mery F, Kawecki TJ, 2003. A fitness cost of learning ability in *Drosophila melanogaster*. ProcR Soc Lond B 270:2465–2469.

Miklosi A, Andrew RJ, Savage H, 1997. Behavioural lateralisation of the tetrapod type in the zebrafish (*Brachydanio rerio*). Physiol Behav 63:127–135.

Nislow KH, Folt C, Seandel M, 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. Can J Fish Aquat Sci 55:116–127.

Odling-Smee L, Braithwaite VA, 2003a. The influence of habitat stability on landmark use during spatial learning in the three spined stickleback. Anim Behav 63:701–707.

Odling-Smee L, Braithwaite VA, 2003b. The role of learning in fish orientation. Fish Fish 4:235–246.

Shettleworth SJ, 1998. Cognition, evolution and behaviour. New York: Oxford University Press.

Shettleworth SJ, 2003. Memory and hippocampal specialization in food-storing birds: challenges for research on comparative cognition. Brain Behav Evol 62:108–116.

Smith EJ, Partridge JC, Parsons KN, White EM, Cuthill IC, Bennett ATD, Church SC, 2002. Ultraviolet vision and mate choice in the guppy (*Poecilia reticulata*). Behav Ecol 13:11–19.

Vallortigara G, Rogers LJ, 2005. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. Behav Brain Sci (in press).

Warburton K, 1990. The use of local landmarks by foraging goldfish. Anim Behav 40:500–505.

Wilson DS, Clark AB, Coleman K, Dearstyne T, 1994. Shyness and boldness in humans and other animals. Trends Ecol Evol 9:442–446.